Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

SEX INTERGRADATION IN THE FLOWERS OF MERCURIALIS ANNUA

CECIL YAMPOLSKY

The older observers have repeatedly called attention to various aberrancies in plant structures, and these have been grouped under teratological phenomena. In this general category have been placed many unrelated phenomena as well as unexplainable ones. That has been particularly true with such occurrences as the appearance, upon a part of a plant which normally bore the organs of one sex, of the sex organs of opposite character. In another paper (1919) I have called attention to the fact that we may consider conditions such as the appearance of female flowers or branches on a male plant, male flowers or branches on a female plant, etc., as evidences of sex intergradation by no means uncommon in the plant kingdom.

In continuing my studies on *Mercurialis annua*, especially on the so-called monoecious form, I have observed some very interesting phenomena which appear to shed further light upon the question of sex determination. *Mercurialis annua* is described as appearing in three forms, male, female, and monoecious. The flowers of the female are, as a rule, two-carpeled, although often three-carpeled, and they are borne in clusters in the axils of the leaves. The flowers of the male are borne in interrupted spikes which surpass the leaves. The flowers of the so-called monoecious form (male, female, and hermaphroditic flowers) are borne like those of the female in clusters in the axils of the leaves.

The individual flowers of the three forms are minute and almost inconspicuous. The female flowers are apetalous, green—each carpel with a single ovule—a two-parted stigma which is white, translucent, and with roughened surface. In the instances in which there is either only one carpel or more than two, the stigma is undivided or multipartite depending upon the number of carpels. The carpels have a rough appearance due to the presence of characteristic translucent hairs. There are also two nectaries. The male flowers are apetalous with 8 to 20 stamens. Each stamen consists of a two-sacked yellow anther and a slender filament. The hermaphroditic flowers are like the female flowers with stamens borne from the bases of the carpels.

In a preceding paper (1919) I have reported upon the appearance of sporadic male flowers upon the female plants and of female flowers upon the male plants. Upon the female plants I have also noted and described various kinds of hermaphroditic flowers. Such flowers have also been observed on the so-called monoecious form but in much greater numbers.

Figures 1 to 7 of Plate V show a few of the forms that I have found. Figure 1 is a diagrammatic representation of a two-carpeled female flower showing (*s*) stigma, (*n*) nectary, and (*t*) hair. The appearance of the stigma and the hairs is particularly characteristic of the flower. Figure 7 is a diagrammatic representation of a male flower with several stamens, the dotted areas representing the anther sacs. In the female flowers there is never any evidence of an aborted or rudimentary stamen, nor is there any evidence in the male flower of an aborted or rudimentary pistil. Figure 2 is a diagrammatic representation of a very common type of hermaphroditic flower. The female elements are in all respects like those in the female flower. The male elements, the stamens, may arise at any point from the base of the carpel. The pollen grains are viable, and under favorable conditions self-pollination occurs and seed is set. In the light of what follows we may assume that the flower represented by figure 1 is more female than the flower represented by figure 2, in which the addition of a single stamen has added a characteristic of the male flower. Figure 3 shows a condition that is also quite common, an hermaphroditic flower with two stamens. These hermaphroditic flowers, too, are self-fertile, and seed is readily set. These flowers may be considered less female than the flowers represented by figures 1 and 2, inasmuch as there is an increase in the male elements. Figure 4 represents a condition in which more than two stamens occur together with the female elements. The number of stamens varies from three to sometimes more than eight. I have found many such flowers which have not been figured. Without sacrificing the functioning power of either the pollen grains or the ovules, various gradations in the proportion of male to female elements are produced in the hermaphroditic flowers. In figure 5 we have a condition in which the male elements have been substituted for half of the female elements. Figure 5 represents a flower with a single carpel, the other half of the flower being occupied by stamens. The number of stamens varies from 4 to 8. This arrangement differs from any described above because there has been a reduction in the amount of the female element so that, at best, the proportion of male and female elements is equal. In this condition, as in the preceding ones, there is no loss in the ability of the pollen or of the ovule to function either in self- or cross-pollination. Figure 6 shows a flower very similar to the one represented in figure 5 but with the addition of one or more stamens arising from the base of the single carpel. In this instance the male elements overbalance the female and the flower is decidedly more male than female. With the male and female flowers as the extremes of a series I have found, in my female and so-called monoecious cultures, intergrading flowers that suggest intergrading degrees of maleness and femaleness. It is interesting to note that this intergradation is not accompanied by sterility as is the case in the transition of ovaries into testes and testes into ovaries in the reported cases in animals.

In the three-carpeled flower I have not found the diversity of intergradation that I have described for the two-carpeled flower. Many of these three-carpeled flowers have been observed with a single stamen, some with two stamens, with three stamens, and with six stamens. The pollen when examined appeared to be perfectly healthy and normal.

While continuing the observations on the above described conditions within the flowers of the so-called monoecious form, an even more striking intergradation of parts, namely pistillody of the stamens and staminody of the pistils, was noted. There were hundreds of flowers that showed such a condition.

Botanical literature abounds with many illustrations of the transmutation of pistils into stamens and of stamens into pistils. The texts on teratology give many illustrations. Without going further into the literature on this subject, I wish to cite the work of Haring (1894). He gives an elaborate series of drawings showing various transition stages of stamens into pistils and of pistils into stamens in *Salix caprea* L. and *Salix cinerea* L. To Haring this facility with which one sex organ is transmuted into another is an indication of the morphological equivalence of sex organs of the opposite sexes.

In the flowers of Mercurialis under observation, most elaborate and varied transition stages appeared of stamens into pistils and of pistils into stamens. Because of the minuteness of the flower, the flower buds were removed and examined under a binocular microscope. Figure 8 represents a female flower with an anther sac growing from one side. As far as could be determined, the ovaries were normal. The pollen grains were for the most part plump and appeared healthy. Figures 9 and 10 are parts of a single three-carpeled hermaphroditic flower. The carpels appeared to be normal; the stamens showed transition stages into pistils. In one stamen (fig. 10) there was one anther sac, in a second one (fig. 9) one of the anther sacs was much reduced in size. There can be no doubt that these stamens had been partially transformed into female tissue, because they showed the white translucent stigmatic surface and the hairs, characteristic of the female flower. The anther sacs were yellow like those of the normal stamens. The pollen from each of the anthers appeared healthy.

Figures 11, 12, and 13 are parts of a two-carpeled hermaphroditic flower with what appear to be two anthers. Figure 11 is evidently a transmuted stamen, showing the stigmatic tissue and the hairs of the female flower. There was no trace of an anther sac or of an ovary. It was completely sterile. The second stamen (fig. 13) had the characteristics of both the stamen and the pistil. It had two anther sacs of unequal size and the stigmatic character and hairs of the pistillate part of the flower. One of the carpels (fig. 12) had imbedded within its tissue an anther sac. The majority of the pollen grains in this sac were plump and appeared normal. This flower, then, showed both staminody of the pistils and pistillody of the stamens in a very marked degree.

Figures 15 to 19 are of a single three-carpeled hermaphroditic flower with four stamens. In only one of the stamens (fig. 15) was there an anther sac. The pollen grains were for the most part plump and appeared healthy. The other three anthers (figs. 16, 17, 18) looked externally like individual carpels although internally there was no evidence of differentiation into fertile and sterile tissue. The three carpels (fig. 19) contained differentiated ovules somewhat enlarged in size and they had an appearance that suggested oedema.

Figures 20 to 22 represent parts of a three-carpeled female flower almost entirely transmuted into stamens. The fact that the flower contained only three parts is evidence that it is a three-carpeled female flower and not a reduced male flower. The pollen grains from each of the sacs showed few shriveled grains.

The male flowers show an equally strong tendency to grade into the female through a series of gradations, from the faintest suggestion of a stigma to the presence of an ovary and of an apparently normal ovule. Figure 24 shows a male flower with ten stamens, two of which have been partially transformed into female tissue, each bearing one anther sac. The remaining eight stamens are normal. Most of the pollen grains in the sacs of the transmuted stamens were normal in appearance.

Figures 25 to 30 represent parts of a single male flower, seven of which were normal, the rest in various stages of transformation. Figure 30 is a normal stamen. Figure 27 represents a stamen with an indication of a stigma, the tissue being white and translucent. The stamen in figure 25 is a little more female, while figures 26 and 29 show more extreme conditions of femaleness. Figure 28 shows a combination of male and female elements, a fully developed stamen and a carpel with a well-developed ovule.

Figure 14 is a part of a male flower much like the one described above, but in which only two stamens were abnormal. The stamen represented by figure 14 had a completely developed ovary (*o*) and two large anther sacs with apparently healthy pollen.

Figure 23 shows a stamen with four anther sacs and a completely developed ovary. This was taken from a flower otherwise male.

It is impossible here to give the numberless variations that occurred in all three kinds of flowers. The illustrations cited give an idea of what is occurring. This evidence of pistillody of the stamens and of staminody of the pistils, coupled with the apparently normal arrangements of male and female elements as seen in figures 1 to 7, emphasize all the more strongly that intergradations within the flowers may occur by steps that are almost insensible. With the female flower as one extreme and the male flower as the other, flowers may grade all the way toward femaleness from the male extreme and all the way toward maleness from the female extreme.

While it has not yet been determined whether or not intergradation is here accompanied by sterility, the indications from the appearance of the pollen and the ovules suggest that total sterility does not occur. Goldschmidt (1916), in his crosses between European and Japanese races of the gypsy moth, *Lymantria dispar*, secured individuals that showed gradations in maleness and femaleness. Such a condition was usually accompanied by sterility. Banta (1916, 1918) finds that in his Crustaceans the more pronounced the sex intergradation the more sterile the form became. While a flower of a plant may not be compared to an individual like a moth or a Crustacean, it is interesting to note that in plants sex intergradation is not, as a rule, accompanied by sterility. On the contrary, the plants whose flowers were studied showed no diminution in seed production or in general vigor.

The condition of intergradation within a series of flowers on a single plant brings up interesting considerations bearing upon the question of when and how the sex of each flower is determined. The *Anlagen* or determiners, if there be such, must be different for the different flowers according to the arrangement of their parts. It must be borne in mind that in this so-called monoecious form of Mercurialis the sex of the plant changes in the course of the plant's development. The initial flowers are female. Several weeks after germination the young plant produces female flowers, and only female flowers are produced for several months. Then a few male flowers or hermaphroditic flowers appear. These increase in number as the season advances. As far as the whole plant is concerned, there is a periodic alteration of sex. A factorial hypothesis for sex cannot explain these results. It would seem logical to assume that the sex of the flower is determined at the time of its formation and not when the plant of which it is a part is in the fertilized egg stage. Moreover what seems to hold true for such flowers as represented in figure 1 to 7 apparently does not hold for the aberrant conditions I have noted. In the various transitional forms there seems to be no definite factor which determines the sex of the flower; pistil passes into stamen and stamen into pistil at any time in its development. The argument for strict sex segregation is obviously nullified because of the behavior of these forms. The line of demarcation between what is male and what is female is wavering and vague. The evidence brought out here tends to emphasize an epigenetic condition for sex rather than the presence of definitely localized qualitative or quantitative factors.

LITERATURE CITED

Banta, A. M. 1916. Sex intergrades in a species of Crustacea. Proc. Nat. Acad. Sci. 2: 578–583.

——. 1918. Sex and sex intergrades in Cladocera. Proc. Nat. Acad. Sci. 4: 373–379.

Goldschmidt, R. 1916. A preliminary report on further experiments in inheritance and determination of sex. Proc. Nat. Acad. Sci. 2: 53–58.

Haring, J. 1894. Abnorme Kaetzchenbildungen bei *Salix caprea* L. und bei *Salix cinerea* L. Oesterr. Bot. Zeit. 44: 386–387, 415–418.

Yampolsky, C. 1919. Inheritance of sex in *Mercurialis annua.* Amer. Journ. Bot. 6: 410–442.

EXPLANATION OF PLATE V

FIG. 1. Female flower: (*s*) stigma, (*n*) nectary, (*t*) hairs.

FIG. 2. Hermaphroditic flower with one stamen.

FIG. 3. Hermaphroditic flower with two stamens.

FIG. 4. Hermaphroditic flower with more than two stamens.

FIG. 5. Hermaphroditic flower with single carpel, the other half occupied by stamens.

FIG. 6. Hermaphroditic flower with single carpel, the other half occupied by stamens, also two stamens from the base of the single carpel.

FIG. 7. Male flower.

FIG. 8. Female flower with a single anther sac without filament budding out of the side of a carpel.

FIGS. 9–10. Parts of a three-carpeled hermaphroditic flower, the three stamens showing transitional stages.

FIGS. 11–13. Parts of a two-carpeled hermaphroditic flower. FIG. 11. Stamen completely changed into sterile tissue with female characteristics. FIG. 12. Anther sac imbedded within the tissue of one carpel.

FIG. 14. Part of a male flower having anther sacs and (*o*) ovule.

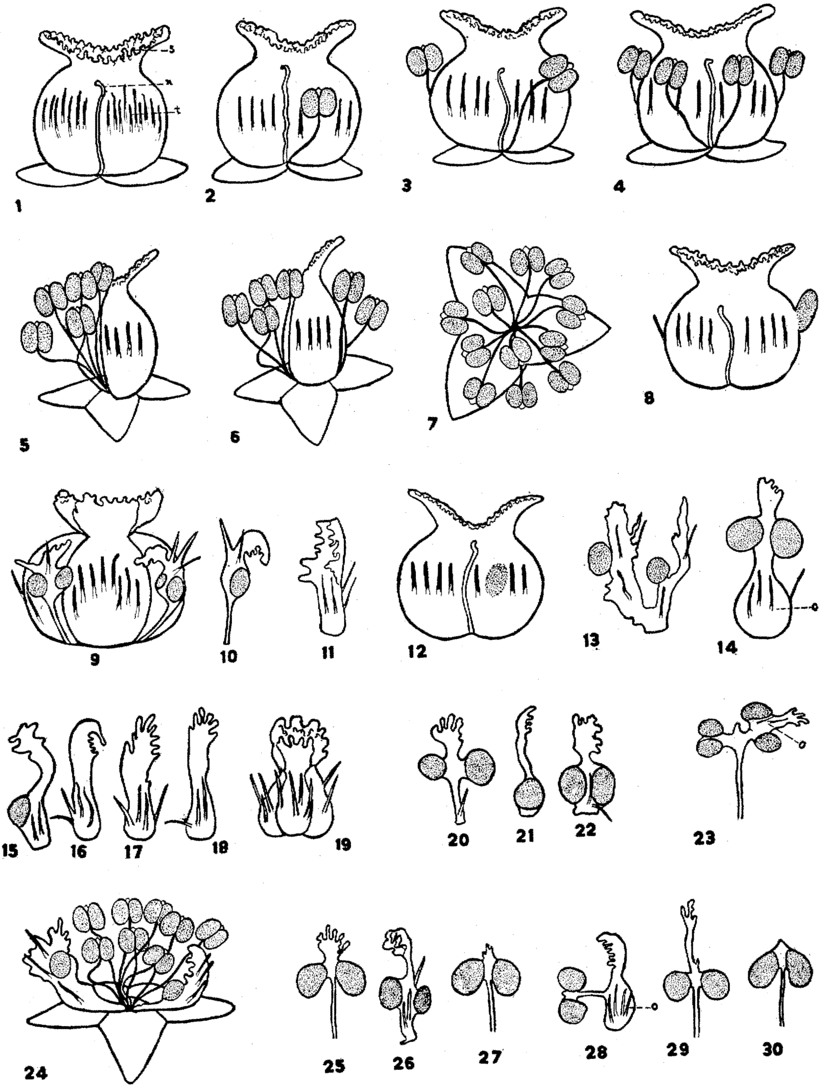
FIGS. 15–19. Parts of a three-carpeled hermaphroditic flower. Figs. 15–18. Transformed stamens: (*as*) anther sacs.

FIGS. 20–22. Parts of a three-carpeled female flower transformed into stamens.

FIG. 23. Stamen with four anther sacs and a single ovule (*o*).

FIG. 24. Male flower with two stamens in transitional stages.

FIGS. 25–30. Parts of a male flower in various transitional stages: (*o*) ovule, (*ns*) normal stamen.



YAMPOLSKY: SEX INTERGRADATION IN MERCURIALIS ANNUA.